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Geographic cline and body size reduction in the Emma field cricket (*Teleogryllus emma*) living on seasonally submerged reservoir slopes

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Abstract

Adult body size often varies geographically in response to local climatic conditions. The Emma field cricket (*Teleogryllus emma*) exhibits a reverse Bergmann's rule pattern, with smaller adults occurring at higher latitudes. This trend was confirmed across populations sampled from 33 °N to 41 °N. One unique population inhabits the periodically exposed reservoir slopes (RS) of the Oishi Dam, Niigata, Japan. These crickets display significantly reduced body sizes compared to those in the surrounding grasslands. To investigate the underlying causes of this body size reduction, we examined the influence of environmental and genetic factors. Laboratory-reared mid-instar nymphs from the RS grew into larger adults than their field-collected counterparts, suggesting an environmental basis for reduced body size. High temperatures led to smaller adults, while high rearing densities (100 individuals per container) significantly reduced adult size compared to low densities (1–2 individuals). Photoperiod (11–16 hours) also influenced growth: longer daylengths extended development and produced larger adults. Small but significant size differences between the RS and surrounding populations suggest possible genetic differentiation, although further genetic analysis is needed to confirm evolutionary divergence. Delayed hatching at the RS exposes the crickets to shorter daylengths, likely accelerating growth and leading to smaller adults. Year-to-year variation in adult head width in the RS population primarily correlated with nymphal densities rather than temperature. Interestingly, smaller adults laid smaller eggs, yet nymphs from these eggs exhibited compensatory growth, often reaching sizes comparable to those from larger eggs, resulting in no significant correlation between adult body sizes of females and offspring. Overall, body size variation in *T. emma* at the RS appears to be shaped by both phenotypic plasticity in response to environmental conditions and genetic differentiation. Despite these fluctuations, body size in some populations has remained stable for over half a century, suggesting possible stabilizing selection or genetic constraints.

Keywords

Adult body size, artificial selection, phenotypic plasticity, photoperiodic response

Introduction

Body size and mass are perhaps the most fundamental organismal characteristics, influencing nearly all aspects of biology (Whitman and Vincent 2008). Various physical and biological factors affect body size (Whitman 2008), and these factors often vary significantly across climatic and geographical locations. While some insects tend to increase in body size at higher latitudes, following Bergmann's rule, others exhibit the opposite trend along latitudinal gradients (Masaki 1967, Tanaka 1991, García-Barros 2000, Blanckenhorn and Demont 2004, Blanckenhorn et al. 2006, Bidau and Marti 2008, Chown and Gaston 2010, Bidau et al. 2016). In insects with variable voltinism, body size may vary in a saw-toothed pattern (Masaki 1973, 1978a, b, 1979, 1983, Johansson 2003, Kivelä et al. 2011), referred to as Masaki's cline (Dingle 1993, Tanaka 2024).

The Emma field cricket *Teleogryllus emma* (Ohmachi & Matsuura, 1951) is distributed widely between 30 °N and 44 °N in the Japanese Archipelago (Masaki 1967). It has a univoltine life cycle and overwinters in the egg stage in a state of diapause throughout its range. Masaki (1967) discovered that body size in this cricket varies greatly along the latitudinal gradient, contrary to Bergmann's rule. He attributed this cline as an adaptation to the length of the growing season and annual mean temperature. Body size increases toward the south as the growing season is longer and annual mean temperatures are higher. This variation is genetically heritable, and similar trends are observed in laboratory-reared crickets, where body size increases with the duration of nymphal development (Masaki 1967, 1978a, Masaki and Walker 1987, Walker and Masaki 1989).

Phenotypic plasticity enables insects to adapt to diverse environments. For instance, the striped ground cricket *Allonemobius fasciatus* (De Geer, 1773) thrives across an altitudinal range of up to 1100 m in North America without significant changes in dia-

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pause intensity, post-diapause development, or nymphal growth despite hatching times differing by as much as 1.5 months (Tanaka and Brookes 1983). Thus, it is essential to determine whether field-observed variations are the result of genetic factors or environmentally induced phenotypic plasticity.

Since its construction in 1978, the Oishi Dam, Niigata, Japan, has controlled water levels seasonally to prevent flooding and generate electricity. The reservoir slopes (RS) are exposed typically from late June to early October (Arai et al. 2024), allowing several species of crickets, including *T. emma*, *Loxoblemmus campestris* (Matsuura, 1988), *Polionemobius mikado* (Shiraki, 1911), *Dianemobius microfasciatus* (Matsumura, 1904), and *Pteronemobius gorochovi* (Storozhenko, 2004), to appear on the slopes. These crickets overwinter as eggs, either submerged underwater or under snow cover, following the seasonal increase in water levels (Ministry of Land, Infrastructure, Transport and Tourism of Japan [MLIT] 1999, Yamaura et al. 1999). Previous studies have reported that *T. emma* exhibits a delayed hatching period on the RS, occurring approximately one month later than in surrounding areas. Furthermore, the adult body size of individuals from the RS was significantly smaller than those from adjacent grasslands, with sizes comparable to those observed in Sapporo, Hokkaido—located 580 km north of the Oishi Dam (Yamaura et al. 1999). This raises a fundamental question: Is this body size reduction driven by environmental constraints, genetic differentiation, or a combination of both?

Recently, Arai et al. (2024) compared the nymphal period under laboratory conditions between the reservoir slope population and a population from the Arakawa riverside located 7 km from the Oishi Dam. They observed substantial differences in the mean nymphal period between the two populations: the former developed significantly faster than the latter. They also reported a significant difference in the body size of field-collected adults between the two populations. Based on these results, Arai et al. suggested that this cricket might be in the early stages of speciation. Insects often evolve rapidly in response to environmental changes such as temperature (Ito and Takahashi 2022), pesticides (Hodjat 2024), and predation pressure (Cook and Saccheri 2013, Zuk et al. 2006). In particular, urban environments (Battles et al. 2024), global warming (Matsuda et al. 2018), and human-induced factors (pesticides and pollution) are known to accelerate genetic and evolutionary changes in insects. However, under laboratory conditions, the differences in head width between the two populations of *T. emma* were smaller than in field-collected specimens. This suggests that the reduced growing season at the RS (due to water-level control) strongly influences nymphal development, but has little impact on the genetic systems controlling body size.

Laboratory studies have shown that various developmental, morphological, and physiological traits in crickets are influenced by environmental factors such as temperature, photoperiod, quality and quantity of food, and crowding as well as by genetic factors (Alexander 1968, Tauber et al. 1986, Danks 1987, Walker and Masaki 1989, Saunders et al. 2002).

This study explored the potential factors influencing adult body size in *T. emma* to understand why adult body size is reduced at the RS of the Oishi Dam. First, we investigated seasonal nymphal development patterns and adult body size in geographically separated populations and in crickets on the RS and in surrounding locations. To identify the factors influencing body size, we exposed cricket nymphs to varying conditions, including temperature, rearing density, and photoperiod, and compared their adult body sizes. Additionally, adults were collected from the RS and the surrounding locations in different years to determine whether their body size changed depending on the year or factors other than submergence. By integrating ecological and experimental approaches, this study aimed to clarify the relative contributions of phenotypic plasticity and genetic factors in shaping body size in *T. emma*. Our findings provide insight into how seasonal environmental constraints, such as periodic submergence, may drive evolutionary changes in insect populations.

Materials and methods

Collection sites.—In addition to the two collection sites at the RS1 and RS2 nymphs and adults of *T. emma* were collected from open grasslands in four prefectures: Hirosaki, Aomori; Sekikawa (SK1, SK2, SK3), Niigata, Tsukuba, Ibaraki, and Saga, Saga (Table 1). The collection sites ranged in latitude from 33.2°N to 40.6°N, with similar longitudes (130.3°E to 140.5°E) and elevations below 200 m. Nymphs and adults were also collected in grassy areas at two sites—Oishi Downstream Park (OP) and Higashimata Botanical Park (HP)—around the Oishi Dam over one or two days (see Fig. 1).

Cricket density in the field appeared low, though precise estimates were not attempted. Crickets were typically collected by pressing down grass underfoot to prompt them to walk or jump into an insect net. The collection sites and annual temperatures are summarized in Table 1. Lake Oishi is located at 38.0°N, 139.6°E. Temperature data for RS1 and RS2, OP, and HP were unavailable. Instead, we used temperature data from Nakajyo (38.0°N, 139.4°E, elevation 14 m; Japan Meteorological Agency 2024) for Sekikawa, the nearest meteorological station to Lake Oishi, adjusted for elevation by subtracting 0.6°C (Kullman 2018).

RS1 and RS2 are exposed areas where grasses grow 30–50 cm tall in summer (Fig. 2A,B). OP lies north of the dam (Fig. 1A, B), with most of the area shaded in the afternoon. Similarly, HP is surrounded by mountains on all sides except the west side facing the lake. This site includes a grassy area under trees where crickets were collected (Fig. 2C). Consequently, both OP and HP receive direct sunlight for only a limited time daily. The grasslands of SK1

Table 1. *T. emma* collection sites. Two reservoir slope sites (RS1, RS2) are submerged annually and exposed from June to September. Temperature data retrieved from the Japan Meteorological Agency (2024).

Sites of collection	Latitude (°N), Longitude (°E)	Abbreviation	Elevation (m)	Submerged	Annual air temperature (°C)
Hirosaki, Aomori	40.6°N, 140.5°E	Hirosaki	90	NO	10.4
Tsukuba, Ibaraki	36.1°N, 140.1°E	Tsukuba	22	NO	14.0
Saga, Saga	33.2°N, 130.3°E	Saga	3	NO	16.7
Sekikawa, Niigata	38.1°N, 139.6°E	SK1, SK2, SK3	29–167	NO	12.9
Reservoir Slope, Niigata	38.0°N, 139.6°E	RS1, RS2	150–160	YES	-
Oishi Downstream Park, Niigata	38.0°N, 139.6°E	OP	129	NO	-
Higashimata Botanical Park, Niigata	38.0°N, 139.6°E	HP	192	NO	-

and SK2 are fully exposed, with grass heights of 20–50 cm high in summer. Crickets were also collected from the riverside of the Arakawa River (SK3), 7 km northeast of Lake Oishi. This site (not shown in Fig. 1) was also considered part of Sekikawa (SK).

To assess year-to-year variations in adult body size, adults were collected at RS2 and the three SK sites during the fall seasons of 2004, 2013, and 2016. A parallel long-term study was conducted in Tsukuba, where an average of 84 female adults were collected at night over approximately 10 days each fall between 2012 and 2024 to evaluate potential size fluctuations. These individuals were primarily found on paved paths along grasslands, with relatively few males observed.

Body size measurements.—Adult body dimensions, including head width, hind femur length, and ovipositor length, were measured using a digital caliper to the nearest 0.1 mm or a micrometer installed in a binocular microscope. Specimens collected in summer included nymphs at different instars. They were classified into last instar, penultimate instar, and earlier instars based on wing pad size and position (MLIT 1999). Head widths were measured 2 or 3 days post-collection.

Rearing conditions.—Nymphs collected from various locations around Lake Oishi on July 31 and August 1, 2013, were transported to laboratories in Tsukuba or Minoh on August 2. Head widths were measured as described above, and they were reared in large tanks (26 × 36 × 30 cm) with mesh covers, each containing 70–100 nymphs. Rearing conditions were maintained at 30 ± 1 °C with a photoperiod of 14 hours light and 10 hours dark (LD 14:10). The nymphs were fed insect pellets (Oriental Kobo Co., Japan) and eggplant slices and provided water in 50-ml vials plugged with absorbent cotton. Adult emergence was monitored daily, and body dimensions were measured the day after emergence.

To investigate the effects of temperature and rearing density on adult body size, nymphs from RS2 were divided into three groups with similar instar compositions. Two groups were reared in small transparent plastic tanks (17 × 32 × 25 cm) at different temperatures: 35 ± 1 °C (N = 60) and 30 ± 1 °C (N = 100). The third group of 100 individuals was reared individually in plastic containers (10 cm in diameter, 6 cm in height) at 30 ± 1 °C. Food and water were provided as previously described, and body dimensions were measured after adult emergence.

To examine the effects of rearing density, adults collected at RS2 in 2006 were allowed to lay eggs in moist sand at room temperature in the Minoh laboratory. Eggs were kept at 25 °C for three weeks and then chilled at 7 °C until the following May. In May, the eggs were incubated at 25 °C to facilitate hatching. Newly hatched nymphs were reared either singly (N = 40) or in groups of 2 (50 replicates) or 100 (4 replicates) near windows at room temperature from May to August 2007. The mean temperature at Minoh during this period was estimated at 24.0 °C (SD = 2.9 °C; Climatic data 2023). Daylengths, including a 1-hour twilight, ranged from 14.9 to 15.5 hours, with an average of 15.3 hours (Japan Meteorological Agency 2024, National Astronomical Observatory 2017). To investigate the effect of changes in rearing density on adult body size, some nymphs initially reared in a group of 100 (4 replicates) were transferred to a group of 25 (8 replicates) after six weeks, and the remaining (14–24 per replicate) nymphs were discarded. Nymphs reared individually (N = 40) or in pairs (50 replicates) were

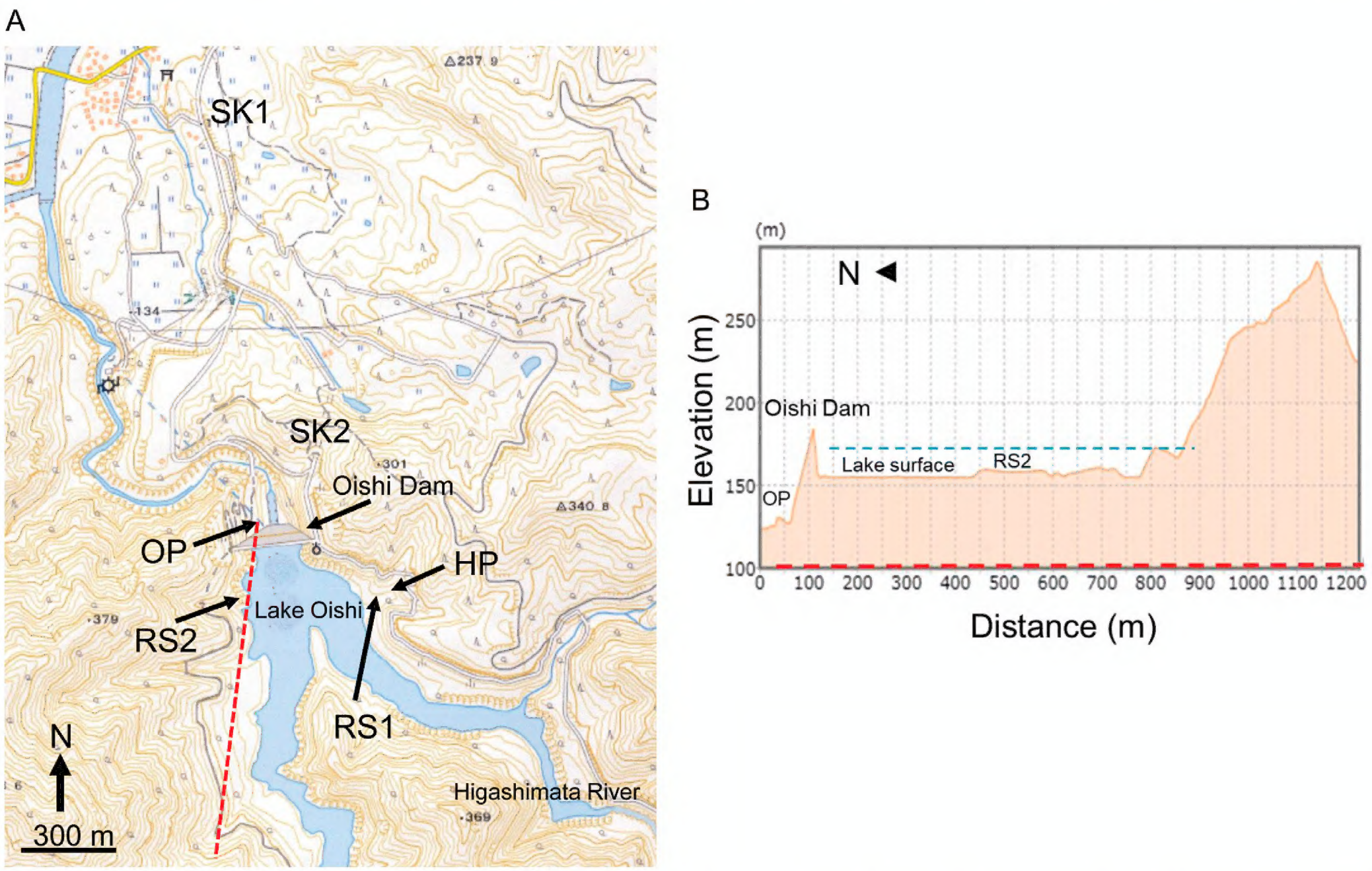

Fig. 1. Map of the collection sites around the Oishi dam (**A**), and a cross-sectional view (**B**) along the red dotted line shown in (A) (based on a web topographic map by Geospatial Information Authority of Japan). For details of the sites, see Table 1.

housed in medium-sized plastic containers (13 cm in diameter, 7 cm in height) equipped with two pieces of folded 11-cm filter paper, food, and water, all placed on sterilized sand. Nymphs kept in groups of 100 (4 replicates) or 25 (8 replicates) were housed in large plastic cases (18 × 28 × 17 cm) containing two pieces of tissue paper, food, and water placed on dry sphagnum moss (2 cm, depth). Water was provided in vials plugged with absorbent cotton. Upon adult emergence, the nymphal period was recorded, and adult head width was measured using an ocular micrometer (1 mm = 14 micrometer units). Similar experiments were conducted using crickets from Tsukuba, where nymphs were reared under different conditions. In one experiment, nymphs were reared singly (N = 50), in pairs (50 replicates), or in groups of 10 (10 replicates) in small plastic containers (9 cm in diameter, 4.5 cm in height) at 30 ± 1 °C under LD 14:10 h at the Tsukuba laboratory. In another experiment, nymphs were reared in groups of 50, 100, and 1000 in large tanks at room temperature, which was monitored hourly with a thermo-recorder (Ondotori 52i, TandD Co, Japan, mean ± SD: 29.6 ± 2.5 °C; range: 22.0–44.3 °C) between July 12 and September 25. Only one tank was used for each density. In the first experiment, containers included two pieces of folded 6-cm filter paper, food, and water vials (30 ml), and groups of 10 were transferred to larger containers (12.5 cm in diameter, 7.5 cm in height) after 21 days. In the second experiment, three pieces of folded newspaper (27 × 40 cm) were provided for shelter.

The effects of photoperiod on nymphal development and adult body size were examined using various photoperiods (LD 11:13 h to LD 16:8 h) at 28 ± 1 °C for the first two laboratory generations (G1 and G2) at the Yamaguchi laboratory. Eggs laid in moist sand by adults collected at RS2 in 2004, as well as those laid by G1 adults, were incubated at 25 °C for three weeks and then chilled at 7 °C for approximately 8 months to terminate embryonic diapause. Subsequently, the eggs were kept at 25 °C for hatching, and the nymphs were reared in 2-L glass beakers (20 nymphs per beaker) with a mesh cover at 28 ± 1 °C. The data from each treatment were pooled for analysis. Head width was measured as previously described. The data for the G2 generation at LD 11:13 h and LD 16:8 h were derived from Arai et al. (2024).

Correlation between female body size and offspring size.—To examine potential maternal effects, 41 female adults collected in September 2012 in Tsukuba (G0) were individually housed in

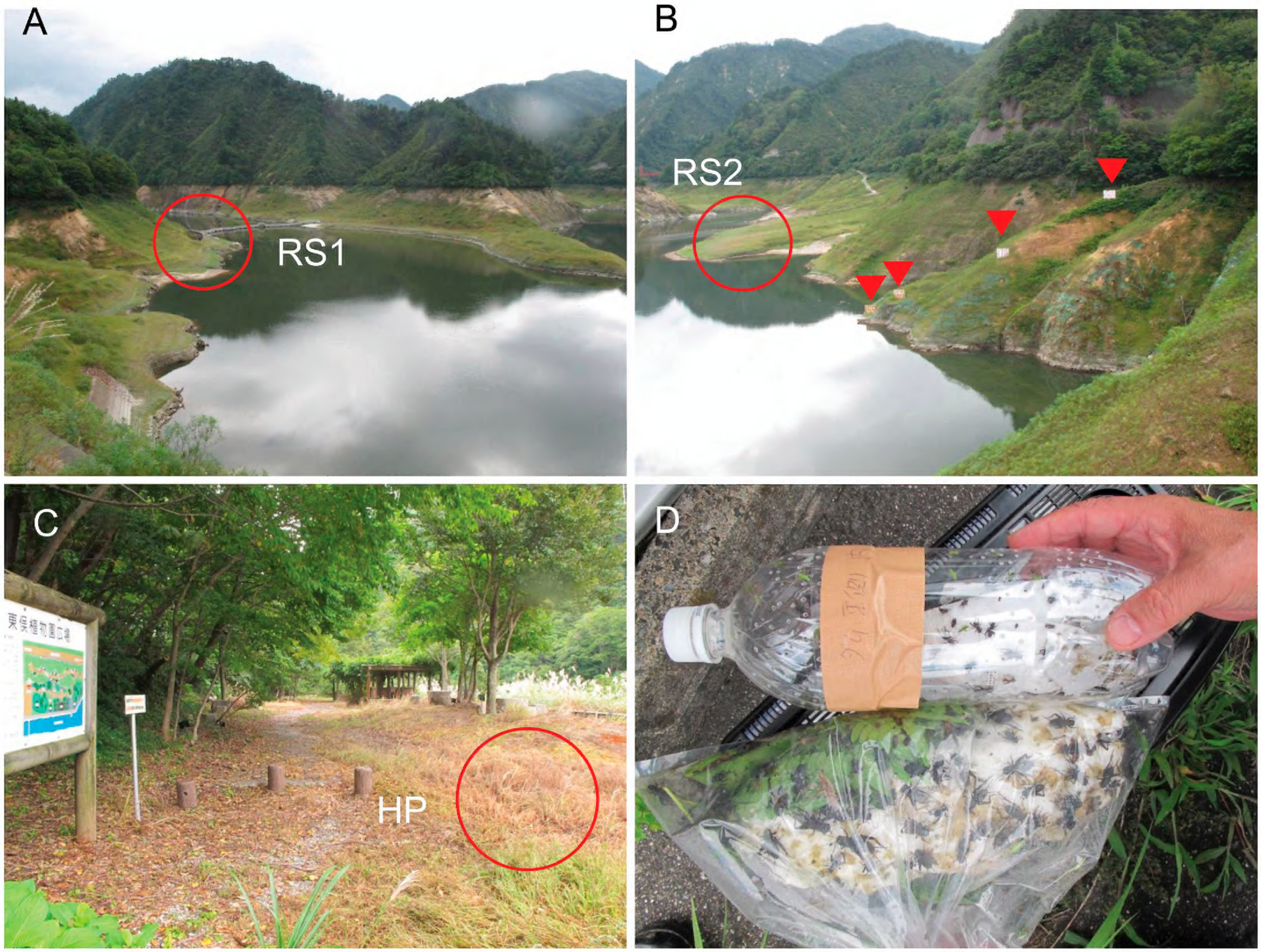

Fig. 2. Photographs showing collection sites and collected crickets. **A.** Reservoir slope 1 (RS1); **B.** Reservoir slope 2 (RS2); **C.** Higashimata botanical park (HP); **D.** Crickets collected at RS1 (top) and Sekikawa (bottom). Note the size differences of crickets between the two samples. Red circles in **A**, **B**, and **C** indicate collection areas. Four red triangles in (**B**) indicate signs showing different elevations: 155 m, 160 m, 170 m, and 180 m above sea level.

plastic containers (15 cm in diameter, 10 cm in height) with mesh covers. They were allowed to lay eggs in moist soil held in plastic cups (100 ml in capacity) at 30°C under a photoperiod of LD 14:10 h. Most females had mated before collection, but no information was available about the mated male(s). Eggs were obtained from 29 females and weighed one month later after reaching the diapause stage and absorbing water (Masaki 1960, Arai and Masuda 2023). For each female, three groups of 9–10 eggs were weighed to the nearest 0.1 mg to examine the relationship between the head width of the female parents and the mean weight of their eggs. The eggs were then chilled at 10°C for 3 months to terminate diapause. Upon hatching at 30°C, 80–100 nymphs from each family line (G1) were reared together in small plastic tanks under the same conditions (30°C, LD 14:10 h). The head widths of adults (18–60 individuals per family) from 22 family lines were measured, as described above, to examine the relationship between the head widths of the female parents and the mean head widths of their offspring. Relationships among the head width of G0 female adults (G0A), egg weight (G1E), and the head width of G1 adults (G1A) were analyzed using log-transformed data. Additionally, the relationship between the head width of G0 adults (G0A) and the growth efficiency (GE) of G1 crickets was examined. GE was defined as the ratio of adult head width to egg weight and calculated as follows: GE = log(G1A/G1E).

Statistical methods.—Adult body dimensions were analyzed using Tukey's multiple comparison test following ANOVA, as well as a *t*-test after evaluating variance homogeneity with an *F*-test. Relationships between adult body sizes and the latitudes of the collection sites and between body sizes of female adults and their offspring were examined using Pearson correlation coefficients. The proportions of different nymphal instars were compared using a χ^2 test. Statistical analyses were conducted with a statistics service available at http://www.gen-info.osaka-u.ac.jp/MEPHAS/kaiseki.html (MEPHAS 2002), Descriptive Statistics (Excel, Microsoft Office 365), or StatView (Statview 1998). Differences were considered significant at $P < 0.05$.

Results

Cline opposite to Bergmann's rule.—Both adult head widths and hind-femur lengths in four geographic populations ranging from 30.24°N to 40.56°N exhibited a high negative correlation with the latitudes for both sexes (Fig. 3). Regression slopes for each trait were similar ($P > 0.05$, Suppl. material 1: table S1), confirming a body size cline opposite to Bergmann's rule, consistent with previous studies (Masaki 1967).

Seasonal development in different populations.—In three populations from Hirosaki, Sekikawa, and Tsukuba, separated by approximately 2°N, similar instar compositions were observed in early–mid August, primarily consisting of penultimate and last instar nymphs (Fig. 4). The proportion of nymphs at these instars was 100%, 81.3%, and 83.8% in the Hirosaki, Sekikawa, and Tsukuba populations, respectively, suggesting that adult emergence occurs in late August in all populations. Southern populations exhibited significantly larger penultimate and last instar nymphs (Suppl. material 1: table S2), supporting the latitudinal size variation pattern.

Body size and seasonal development around Lake Oishi.—Crickets collected from RS1 and RS2 between July 31 and August 1, 2013, were significantly smaller than those from surrounding sites (OP, HP, SK, Fig. 5A). Notably, no penultimate or last instar nymphs were present at the RS, suggesting a delayed hatching time. The large size difference between individuals from the RS and SK was noticeable even at the time of collection (Fig. 2D). Head width was similar between OH and HP penultimate instar nymphs, and their mean values were significantly smaller than those of the SK crickets ($P < 0.05$, Tukey's multiple comparison test, Suppl. material 1: table S3).

When these nymphs were reared to the adult stage in the laboratory (30°C, LD 14:10 h), no significant difference was observed in head width between sexes (*t*-test, $P > 0.05$ for each, Suppl. material 1: table S4), and subsequent analyses were conducted for both sexes combined. Relatively small differences were observed in head width across the four locations, with the smallest value belonging to the crickets from OP and HP (Fig. 5B). Notably,

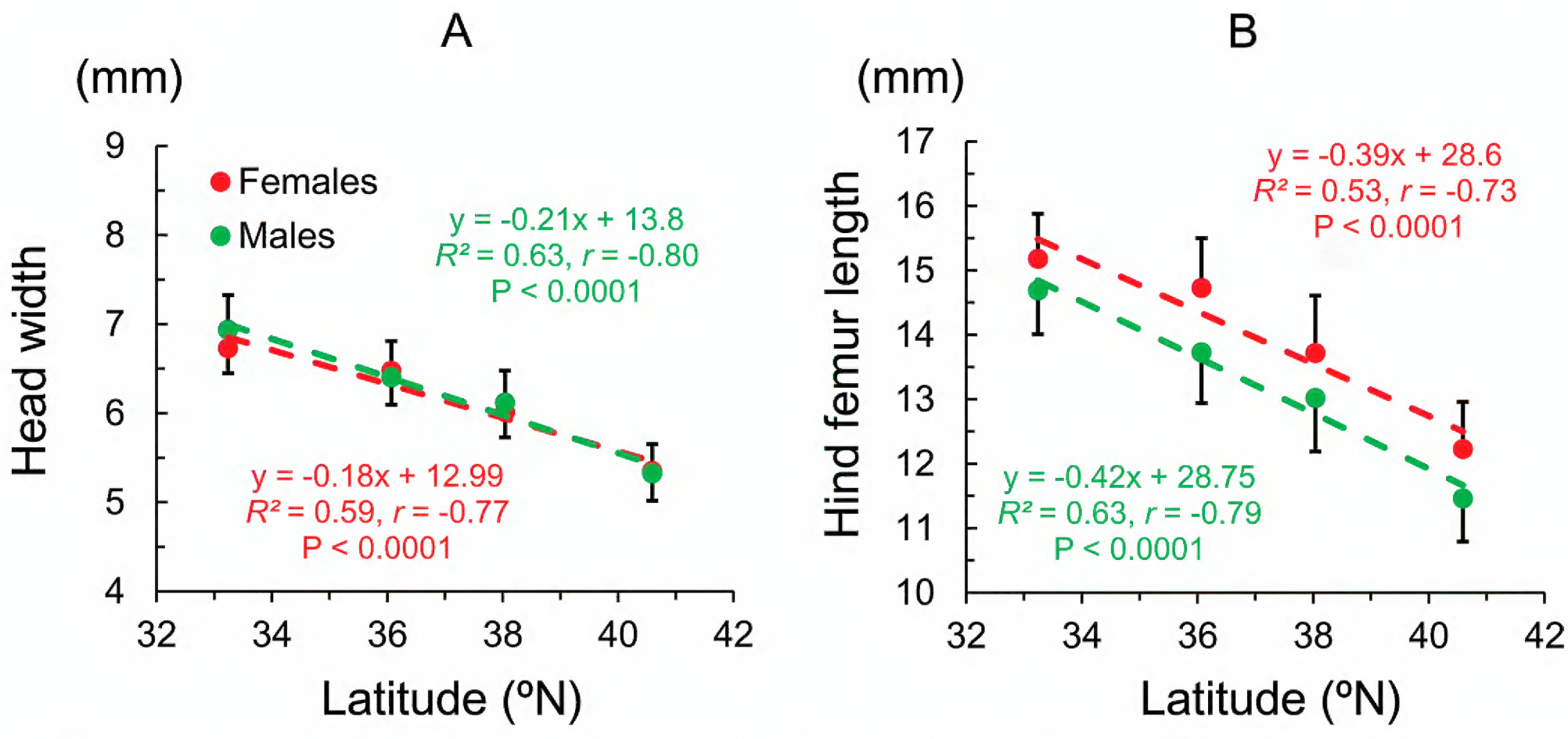

Fig. 3. Head widths and hind femur lengths (mean ± SD, mm) of *T. emma* collected at Saga (33.2°N), Tsukuba (36.1°N), Sekikawa (38.1°N), and Hirosaki (40.6°N). Sample sizes ranged from 32 to 96 (Suppl. material 1: table S1).

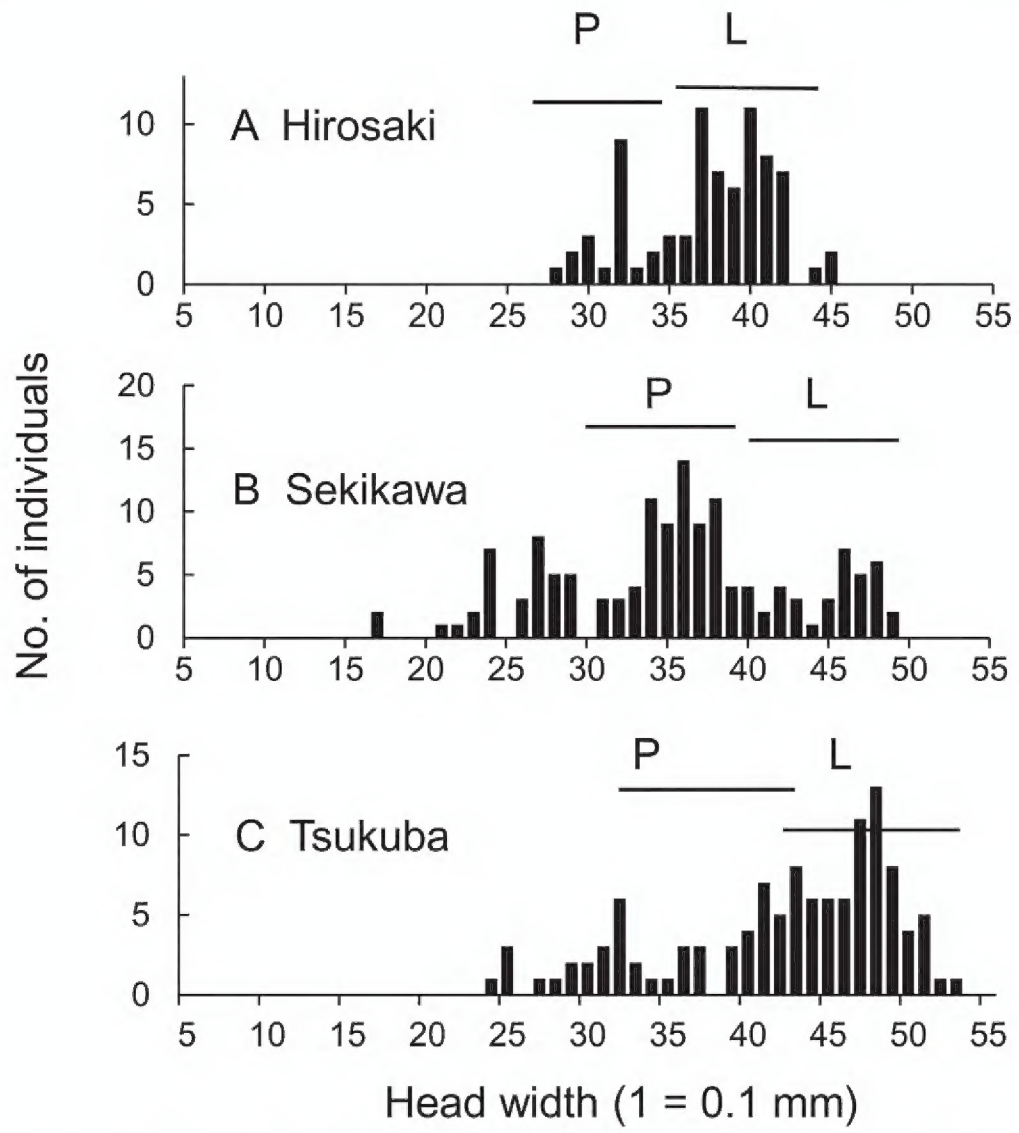

Fig. 4. Head widths of *T. emma* nymphs collected from Hirosaki (**A**), Sekikawa (**B**), and Tsukuba (**C**) during summer 2013. Head widths were measured on August 3 for the Hirosaki population (N = 77), August 2 for the Sekikawa population (N = 139), and August 13 for the Tsukuba population (N = 117). P: penultimate instar; L: last instar.

adults from the RS had a mean head width (mean ± SD = 5.9 ± 0.4 mm, N = 174) close to that of individuals from SK (6.1 ± 0.3 mm, N = 123), although the difference was statistically significant (Tukey's multiple comparison test, $P < 0.05$). Similar patterns were observed for hind femur length and female ovipositor length (Suppl. material 1: table S4).

In contrast, adults directly collected from the field in September demonstrated significant differences: adults from the RS (mean head width ± SD = 4.8 ± 0.4 mm, N = 181) were markedly smaller than those from the other locations (Fig. 5B, Suppl. material 1: table S5). Those from SK showed the largest body size (6.1 ± 0.3 mm, N = 129). Photographs showing typical specimens from SK and the RS are given in Fig. 5C.

The differences between laboratory-reared and field-collected adults reflect the interactions between instar stage at collection and laboratory conditions. Nymphs from SK, collected at later instars, required only 13.4 days on average (SD = 4.2 days, N = 123) to reach adulthood, minimizing laboratory effects (Fig. 5B, Suppl. material 1: tables S4, S5). Conversely, earlier instars collected at the RS required 24.8 days (SD = 3.0 days, N = 174) for adult emergence. The nymphs from OP and HP required 19.3 days (SD = 3.6 days, N = 88) and 17.5 days (SD = 3.4 days, N = 68), respectively. The results clearly demonstrate that RS individuals can reach an adult body size similar to that of SK individuals under certain conditions.

Factors influencing adult body size.—Some nymphs collected at the RS in summer (Fig. 5A) were divided into three groups. Two of these groups were reared at 30°C and 35°C to compare adult body size at different temperatures. The data for both sexes were combined and showed that both head width and hind femur length were smaller at 35°C than at 30°C, although the difference

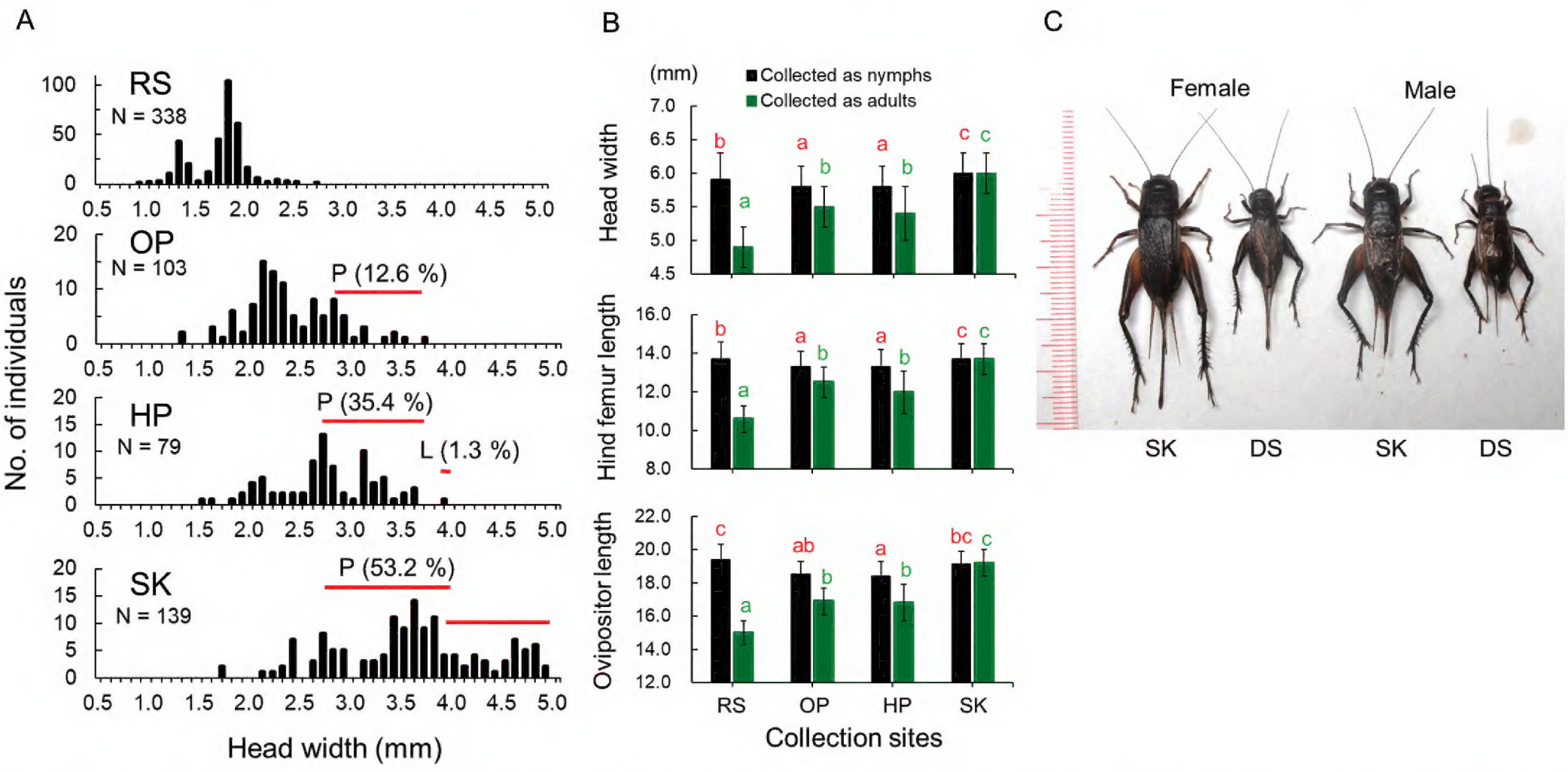

Fig. 5. Body size of *T. emma* nymphs collected around the Oishi dam during summer 2013 (**A**) and reared to adulthood at 30°C under LD 14:10 h conditions (black histograms, **B**). Green histograms in (**B**) show body sizes (mean ± SD, mm) of individuals collected as adults in September, excluding those from Sekikawa (SK), which include both adults collected directly and nymphs reared to adulthood in the laboratory. P: penultimate instar; L: last instar. Percentages in parentheses in (**A**) represent the proportions of individuals at the penultimate (P) or last (L) instar (based on Suppl. material 1: table S3). Other sampling sites: RS, reservoir slope; OP, Oishi downstream park; HP, Higashimata botanical park (see Table 1). Typical specimens collected at SK and RS are shown in (**C**). Different letters in (**B**) indicate significant differences among collection sites in each series, based on Tukey's multiple comparison test ($P < 0.05$).

in head width was only marginally significant (Fig. 6A, B; Suppl. material 1: table S6).

Nymphs in the third group were reared individually to examine the effect of rearing condition—individual vs. group—on adult body size at 30°C. Nymphs reared individually (mean = 27.6 days) took longer to mature than those reared in a group (mean = 24.9 days), but the difference was statistically insignificant (*t*-test, P = 0.15, Suppl. material 1: table S6). There was no significant difference in head width or hind femur length between these groups (P > 0.05, Fig. 6C).

Further experiments with RS nymphs reared at different densities showed that individuals reared in groups of 100 produced significantly smaller adults than those reared singly or in pairs (Tukey's multiple comparison test, P < 0.05, Fig. 7A). Interestingly, transferring nymphs from high-density groups to lower density (25 per container) after six weeks (approximately two-thirds of the nymphal period) eliminated size reductions, suggesting that late-stage density influences adult size more than early-stage density. Nymphal development was similar in all treatments except for those reared in pairs (Fig. 7B, Suppl. mate-

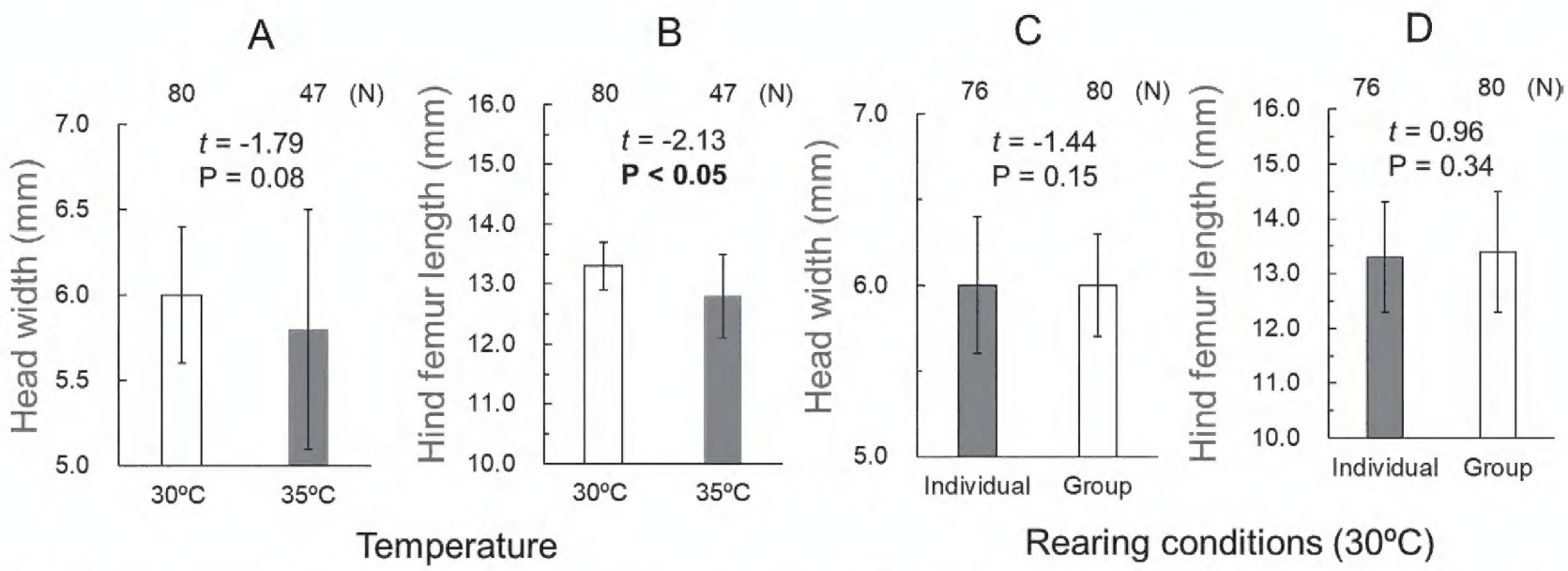

Fig. 6. Effects of temperature and rearing density on adult body size in *T. emma*. Adult head width and hind femur length were measured for individuals collected as mid-instar nymphs from the reservoir slope (RS) in summer 2013. Nymphs were reared in groups to adulthood at 30°C and 35°C under LD 14:10 h conditions (**A, B**) or reared individually at 30°C (**C, D**). The values for group-reared adults in (**C**) and (**D**) were derived from (**A**) and (**B**). Bold letters indicate significant differences (P < 0.05).

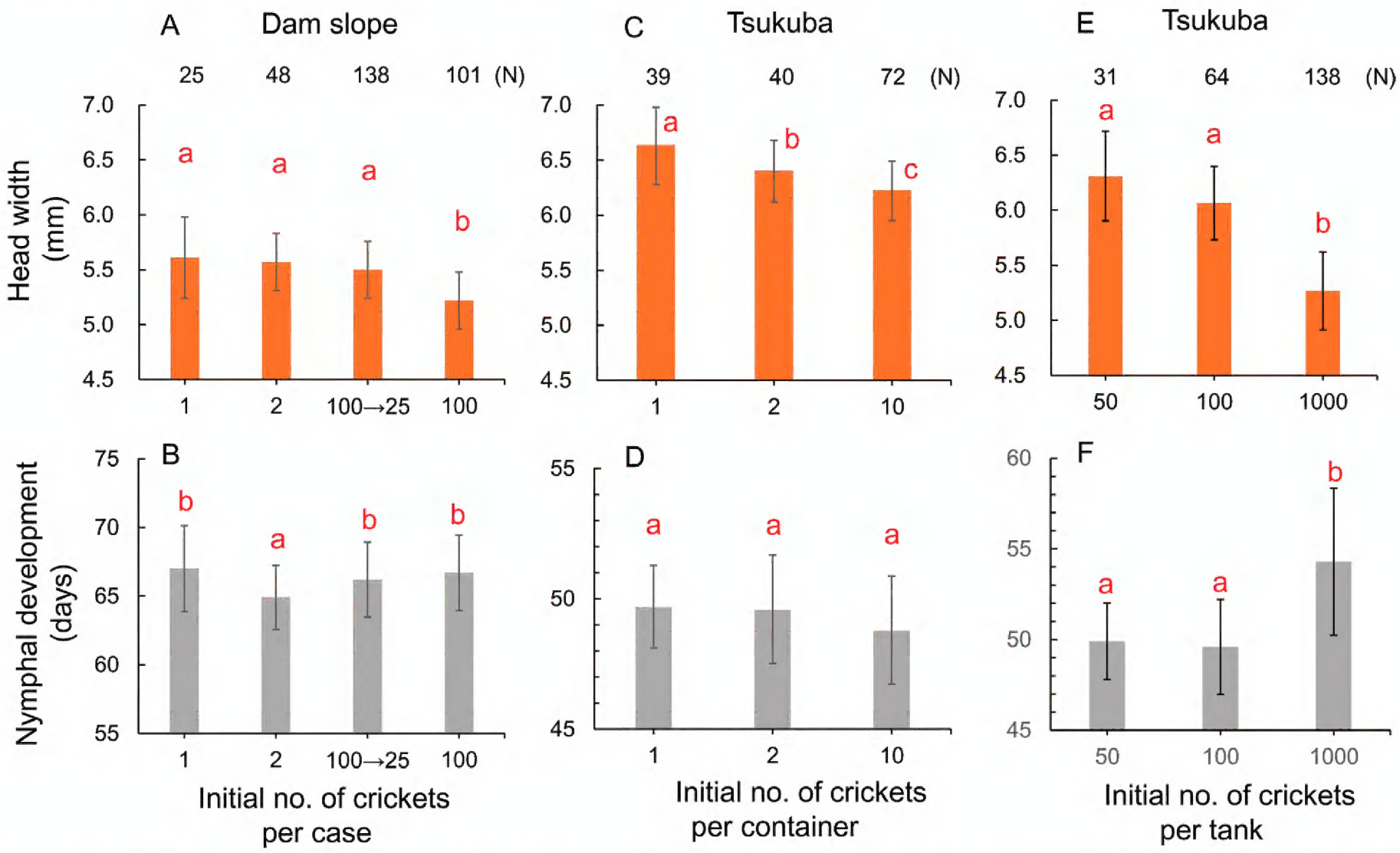

Fig. 7. Effects of rearing density on adult head width (mean ± SD, mm) and nymphal development time (mean ± SD, days) in *T. emma* from the reservoir slope (RS) and Tsukuba. Nymphs from RS were reared singly, in pairs, or in groups of 100. Some nymphs initially reared in groups of 100 were transferred to a group of 25 after 3 weeks. These experiments were conducted from May to September 2017 at a mean temperature of 24.0°C under semi-natural daylengths ranging from 14.9 to 15.5 hours (**A, B**). Nymphs from Tsukuba were reared singly, in pairs, or in groups of 10 (**C, D**) at 30°C under a photoperiod of LD 14:10 h in 2013. Additionally, they were reared in groups of 50, 100, and 1000 by windows at room temperature (mean = 29.6°C, SD = 2.5°C) in 2024 (**E, F**). Different letters indicate significant differences among treatments based on Tukey's multiple comparison test (P < 0.05). For detailed data, see Suppl. material 1: table S7.

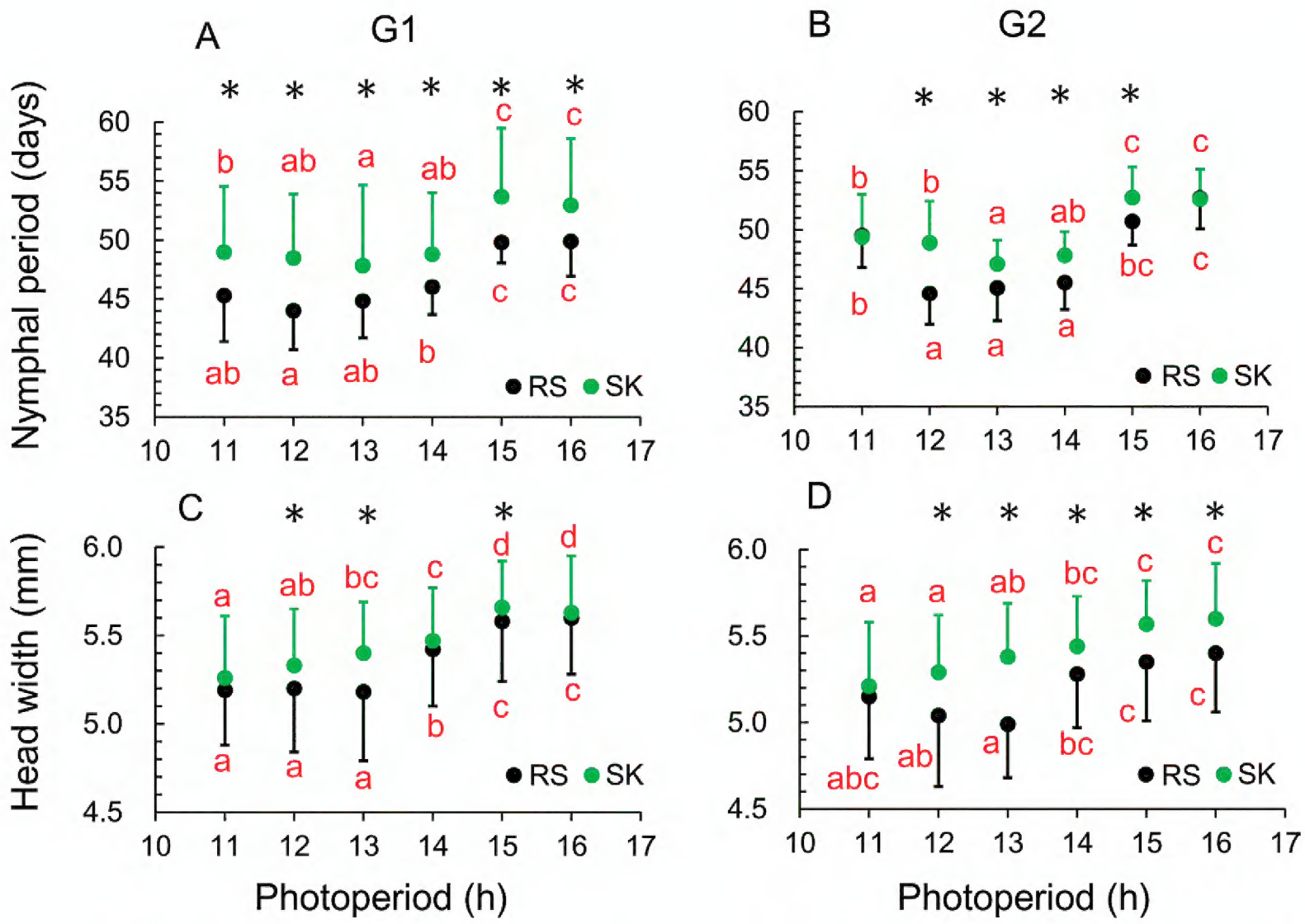

Fig. 8. Photoperiodic responses at 28°C. Mean values and one standard deviation (SD) of the nymphal period (days) and adult head width (mm) are shown for G1 (**A, C**) and G2 (**B, D**) of *T. emma* crickets from the reservoir slope (RS) and Sekikawa (SK) populations. Different letters indicate significant differences among photoperiods within each population, as determined by Tukey's multiple comparison test ($P < 0.05$). Asterisks denote significant differences between the two populations at each photoperiod, based on a *t*-test ($P < 0.05$). For sample sizes, refer to Suppl. material 1: table S8. The data at 11 and 16 h photoperiods are derived from Arai et al. (2024).

rial 1: table S7). Similar results were observed in nymphs from Tsukuba. In one experiment, adult body size tended to decrease slightly as rearing density increased from 1 to 10, while the duration of nymphal development remained consistent across the three treatments (Fig. 7C, D). In another experiment, nymphs reared in groups of 50 and 100 showed similar adult body sizes and nymphal development durations, whereas those reared in groups of 1000 had significantly smaller adult head widths and delayed nymphal development (Fig. 7E, F; Suppl. material 1: table S7).

Comparison of photoperiodic responses.—RS and SK nymphs reared under photoperiods ranging from LD 11:13 h to LD 16:8 h developed more rapidly under shorter photoperiods than under longer photoperiods (Fig. 8A). This pattern was observed in both G1 and G2, indicating a short-day type of response. The slight differences between the two generations in G2 may be attributable to the smaller sample sizes (Suppl. material 1: table S8). In both generations, RS nymphs developed more rapidly than SK nymphs (*t*-test, $P < 0.05$) across all photoperiods except for LD 11:14 h and LD 16:8 h in G2. Adult head width also varied with photoperiod in both G1 and G2 (Fig. 8B, Suppl. material 1: table S8). Small but significant differences in mean head width were detected between the two populations at certain photoperiods (*t*-test, $P < 0.05$). Additionally, a strong positive correlation was found between the mean duration of nymphal development and adult head width ($r = 0.75$, $P < 0.0001$, Fig. 9). These results suggest that longer nymphal development durations lead to larger adult body sizes and suggest genetic differentiation between the RS and SK populations.

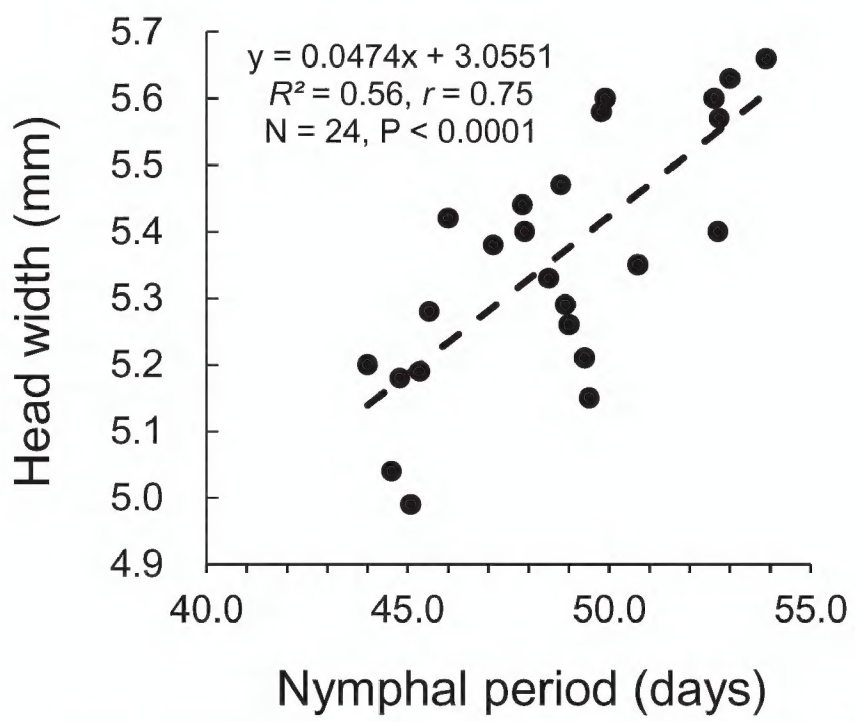

Fig. 9. Relationship between nymphal development and adult body size in *T. emma* reared under photoperiods ranging from LD 11:13 h to LD 16:8 h at 28°C. Data points represent the mean values for the reservoir slope (RS) and Sekikawa (SK) populations, as summarized in Suppl. material 1: table S8.

Year-to-year variation in adult body size at RS and SK and in Tsukuba.—Head width measurements for RS and SK adults collected in 1999, 2004, 2013, and 2016 revealed consistent differences: RS crickets were smaller, but their mean size fluctuated across years (Fig. 10A, Suppl. material 1: table S9). In contrast, SK crickets remained relatively stable across the same period, suggesting that RS size variation is driven by local environmental factors rather than regional climate trends.

In Tsukuba, head widths of crickets collected from 2012 to 2024 fluctuated significantly (Fig. 10B). The variation was not significantly correlated with the mean air temperature during the growing season (May–August), although the latter showed an increasing trend over the years (r = 0.83, N = 6, P < 0.05, Suppl. material 1: table S10C). The results suggest that non-meteorological factors may drive size fluctuations at Tsukuba.

Relationships between female body size and offspring size.—A significant correlation was observed between the head widths of field-collected female adults and the mean weight of their eggs (r = 0.48, N = 29, P < 0.05, Fig. 11A, Suppl. material 1: table S11), suggesting that larger females tend to produce larger eggs. In the analysis in Fig. 11B–D, data points from the largest 11 and smallest 11 G0 females were distinguished using closed and open symbols, respectively. As summarized in Table 2, the large group (composed of significantly larger G0 females than the small group) produced larger eggs. A significant positive correlation was also found between egg size and adult head width in G1 (Fig. 11B, r = 0.45, N = 44, P < 0.05), suggesting that adults from larger eggs attained larger body sizes.

Unexpectedly, however, there was no significant correlation between the adult head widths of G0 females and their G1 offspring (Fig. 11C, r = -0.02, N = 44, P = 0.88). These results suggest that while larger females produce larger eggs and nymphs from larger eggs grow into larger adults, differences in G0 female body size are not directly reflected in the adult body size of their G1 offspring. This phenomenon may be related to the considerable variation in egg weights, regardless of the female parent's body size (Fig. 11B), with no significant difference in mean values between the two size groups (t-test, P > 0.05, Table 2). Additionally, the growth efficiency, the logarithmic ratio of G1 head width to egg weight (Log(G1A/G1E)), showed a significant negative correlation with G0 female body size (LogG0A) (Fig. 11D, Suppl. material 1: table S10, r = -0.43, N = 44, P < 0.05). This suggests that the offspring of smaller females will exhibit higher growth efficiency than the offspring of larger females.

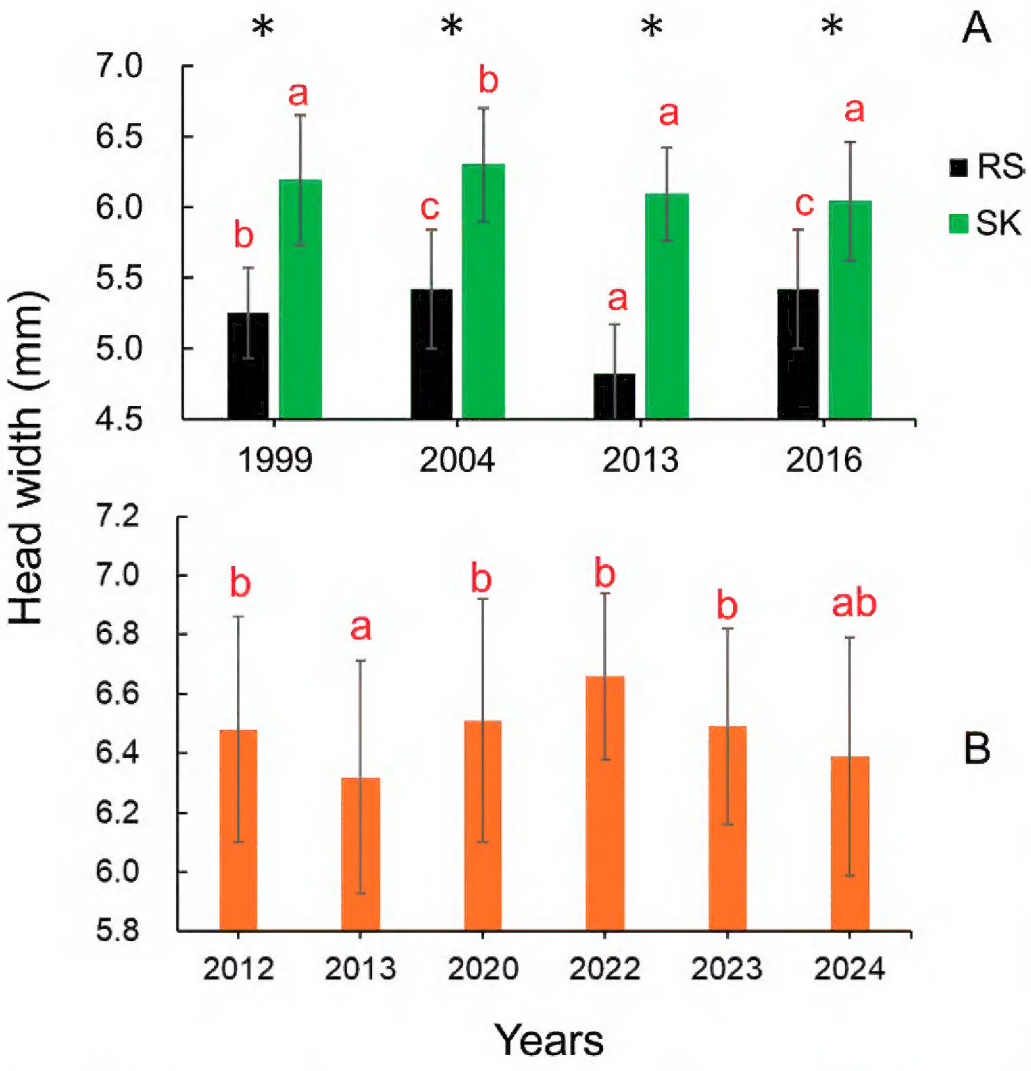

Fig. 10. Fluctuations in the head width of *T. emma* adults from the reservoir slopes (RS) and Sekikawa (SK) across different years (**A**). Different letters indicate significant differences among years within each population, as determined by Tukey's multiple comparison test (P < 0.05). Asterisks denote significant differences between the two populations based on a t-test (P < 0.05). Data from 1999 are based on Yamaura et al. (1999), and data for the RS population in 2013 are sourced from Suppl. material 1: table S5. Fluctuations in the head width of female *T. emma* collected in Tsukuba across different years (**B**). Different letters indicate significant differences among years based on Tukey's multiple comparison test (P < 0.05). Sample sizes range from 25 to 181 in (**A**) (Suppl. material 1: table S9) and from 48 to 104 in (**B**) (Suppl. material 1: table S10).

Table 2. Effects of female *T. emma* body size on egg size and adult body size in the following generation (G1). Field-collected female adults (G0) were divided into two groups consisting of large and small groups based on body size and offspring produced by different females were reared separately at 30°C and LD 14:10 h. Mean ± SD are shown. Bold letters indicate that the difference is significant at P < 0.05.

G0		G0	G1	G1	G1
Female	N	Head width (mm)	Egg weight (mg)	Head width (mm)	Head width (mm)
Body size		Females		Females	Males
Large	11	6.73 ± 0.27	1.23 ± 0.05	5.89 ± 0.22	5.85 ± 0.24
Small	11	6.05 ± 0.20	1.17 ± 0.06	5.91 ± 0.18	5.88 ± 0.18
t-value		9.73	3.80	-0.17	-0.32
P		**< 0.0001**	**0.002**	0.87	0.75

Discussion

Since the construction of the Oishi Dam in 1978, the seasonal submergence and exposure of its slopes have significantly impacted the habitat of *T. emma*. These slopes are exposed from mid-June to early October, allowing grasses to grow 30–50 cm tall and several cricket species, including *T. emma*, to occur (Yamaura et al. 1999, Arai et al. 2024). This exposure period, which corresponds to the growing season of *T. emma* at the RS, is approximately one month shorter than that in surrounding areas and has a marked influence on nymphal development and adult body size.

T. emma exhibits a geographical cline in adult body size opposite to Bergmann's rule, with smaller adults found further north where growing seasons are shorter (Masaki 1967, 1978a, 1996). This study observed a similar cline across populations sampled between 33.2°N and 40.6°N (Fig. 3) and confirmed a strong correlation between nymphal development duration and adult body size (Fig. 9).

Across latitudes, most *T. emma* nymphs reach the penultimate or last instar by early August. According to Masaki (1960), eggs of *T. emma* require 264 degree days above 13.5°C to complete post-diapause development, a value comparable to that of Chinese populations (Suppl. material 2: fig. S1, Zhao et al. 2010). Post-diapause development begins earlier in southern regions, with daily mean temperatures exceeding 13.5°C in late April in Tsukuba, early May in Sekikawa, and mid-May in Hirosaki (Japan Meteorological Agency 2024). Despite latitude-based differences in hatching times, adults may emerge in late August across all populations or slightly earlier at higher latitudes.

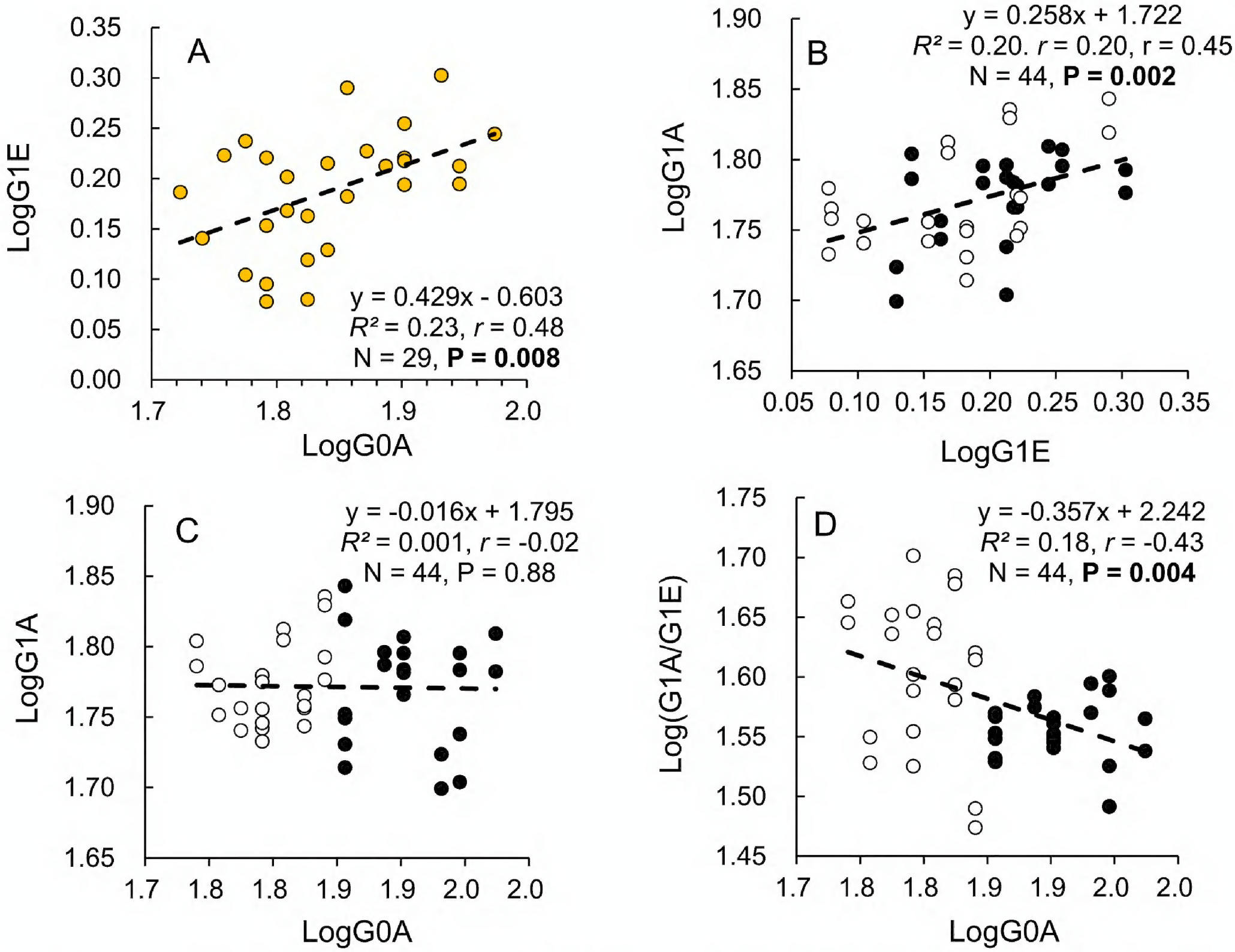

Fig. 11. Log-plots showing the relationships between female adult head width (G0) and offspring body size (G1) in *T. emma* from Tsukuba. **A.** Relationship between the head widths of female adults (LogG0A) and the weights of their eggs (LogG1E). **B.** Relationship between mean egg weight and head width of male and female adults in 22 family lines reared at 30°C under LD 14:10 h conditions (LogG1A). **C.** Relationship between the head width of G0 females and G1 male and female adults across 22 families. **D.** Relationship between the head width of G0 females and Log(G1A/G1E). In panels (**B–D**), data points from the largest 11 and smallest 11 G0 females were represented using closed and open symbols, respectively. Egg weight represents the average of three groups of 9–10 eggs per female. G1 adult head width data are based on an average of 23.5 males and 17.8 females per family; however, similar trends were observed when analyzing each sex separately (see Suppl. material 1: table S11).

In contrast, at the Oishi Dam, nymphal body sizes in early August varied by location (Fig. 5), reflecting differences in hatching timing. RS crickets hatch about one month later than SK3 crickets (Arai et al. 2024). Intermediate body sizes were observed at OP and HP, likely due to partial shading and intermediate hatching times. OP, located north of the dam, and HP, surrounded by mountains and shaded by trees, provide earlier hatching conditions than the RS but later than SK. Genetic differences among crickets from these locations merit further study to understand their adaptation to local environments.

Arai et al. (2024) reported faster growth and smaller adult sizes in RS crickets under controlled conditions, suggesting genetic differences. However, this study observed less pronounced adult size differences compared to nymphal development periods under laboratory conditions (Fig. 8). Delayed hatching at the RS exposes crickets to shorter daylengths, accelerating growth and reducing adult size. This conclusion aligns with the strong correlation between nymphal development duration and adult body size (Fig. 9).

In this study, we further investigated other potential factors influencing nymphal development and adult body size in *T. emma* to better understand the evolutionary impact of annual habitat submergence on the life cycle of this cricket. Year-to-year variations in *T. emma* adult size were observed at the RS (Fig. 10). During the growing season, from late May to mid-September, the mean air temperature of 10-day intervals at Nakajo, the nearest meteorological observatory to the Oishi Dam (Japan Meteorological Agency 2024), ranged from 24.0°C to 24.6°C, and sunshine hours ranged from 56.0 to 65.9 hours (Suppl. material 1: table S12). Neither temperature nor sunshine hours showed significant variation between the years when crickets were collected. In contrast, SK crickets showed consistent sizes, indicating that non-meteorological factors influence size fluctuations in RS crickets.

Temperature plays a crucial role in regulating development and growth in insects, including crickets (Chapman 1998, Walker and Masaki 1989). When *T. emma* nymphs, collected as mid-instars from the RS in early August, were reared in groups, they grew into smaller adults at 35°C than at 30°C. Although no specific data are available, the habitat at the RS, with no shading objects, likely becomes extremely hot during the day, especially in summer. Furthermore, high nymphal densities in the RS habitat—exceeding 100 individuals per m^2 in some years—could lead to competition for resources, further reducing adult size (MLIT 1999).

Interestingly, adult body size in Tsukuba fluctuated significantly between 2012 and 2024. During this period, annual air temperature significantly increased; however, body size of this univoltine insect showed no significant correlation with either temperature or year (Suppl. material 1: table S10). Similar long-term studies in other orthopterans, such as *Locusta migratoria*, revealed stable body sizes despite significant climate warming over decades (Tanaka 2022). While no noticeable variation in *T. emma* nymphal and adult densities was observed at Tsukuba, formal quantitative estimates of nymph densities were not conducted. Thus, the factors driving annual fluctuations in body size at this location remain unknown.

Matsuda et al. (2018) reported that body size in the lawn ground cricket *Polionemobius mikado* (Shiraki, 1911), which has a uni- or bivoltine life cycle, has changed over the past 40 years at certain latitudes in response to climate warming. Their conclusion was based on relatively small sample sizes (5–14 individuals) collected over three years. In contrast, for the univoltine *T. emma*, Masaki (1967) proposed an equation describing geographic variation in head width as a function of latitude, longitude, and altitude using samples collected over eight years (1959–1964). According to this equation, the estimated female head width in Tsukuba was 6.6 mm. However, our recent data (N = 506; Suppl. material 1: table S11), collected 53–60 years later, show a mean head width of 6.5 mm, indicating minimal change despite a 2.5°C increase in annual mean temperature over the past six decades ($r = 0.82$, $P < 0.0001$, Suppl. material 2: fig. S2). These results suggest that *T. emma* has not responded to climate warming in the same way as *P. mikado*, possibly due to differences in life-history strategies related to voltinism. While stabilizing selection or genetic constraints could explain this size stability in *T. emma*, a more comprehensive statistical analysis incorporating multiple environmental variables is needed to rigorously test these hypotheses. Despite rising temperatures, our findings indicate that *T. emma*'s body size remains largely stable, potentially due to adaptive mechanisms or phenotypic plasticity buffering against environmental variability.

The egg period of *T. emma* shows an increasing trend toward southern regions, which is attributed to an increase in diapause intensity. This variation is considered a climatic adaptation to prevent untimely hatching before winter (Masaki 1978a). Arai et al. (2024), in a comparison of egg periods between the RS and SK populations at various temperatures, found shorter egg periods in the RS population compared to the SK population, suggesting genetic differentiation. This finding implies that diapause intensity may change more easily genetically than adult body size, allowing for the stabilization of the life cycle in local environments.

One potential factor contributing to year-to-year fluctuations at the RS is nymphal density, as noted by Arai et al. (2024). In summer, the RS are uniformly covered with grasses 30–50 cm high, and densities exceeding 100 nymphs per m^2 were recorded in 1999 (MLIT 1999). High densities are likely at the RS because natural predators such as spiders, ants, ground beetles, and mantises, while capable of migrating to the area, are eradicated annually due to submergence. However, unidentified yellow parasitic ticks were frequently observed on adults in 2013 (Suppl. material 2: fig. S3). For example, in early August 1999, nymph density at RS exceeded 100 individuals per m^2, compared to fewer than 10 individuals per m^2 in surrounding areas (Yamaura et al. 1999). Similar levels of abundance were noted in 2004 and 2006, although precise density estimates were not made (Arai T, personal observation). At SK, crickets were typically collected by pressing down grass with a foot to prompt movement into an insect net. In contrast, nymphs at the RS in 2013 were so abundant that hundreds could be captured quickly by sweeping a net through the grass. Ten sweeps on August 1 yielded an average of 32 nymphs (range: 14–47; N = 5; Tanaka S and Arai T, unpublished observation). In 2016, when adult body size increased compared to 2013 (Fig. 5B), heavy rains carried logs and destroyed several grassy areas at the RS, and by September, adult density had dropped to levels comparable to those of surrounding sites (Arai T, personal observation). Future studies should quantify the relationship between cricket density and adult body size to better understand these dynamics.

Egg size is often related to adult body size in insects. In lepidopterans, larvae from smaller eggs typically develop into smaller adults (García-Barros 2000). In *T. emma*, smaller RS adults lay smaller eggs compared to larger SK adults (Arai et al. 2024). However, no significant difference in egg size was observed between the two populations in the subsequent laboratory generation, suggesting that the variation in egg size between the two populations is not genetically determined.

The present study also investigated the maternal effects on offspring body size in *T. emma* crickets (Fig. 10). Smaller field-collected females (G0) produced smaller eggs, and nymphs hatching from these eggs tended to develop into smaller adults (G1). However, no significant correlation was detected between the adult body sizes of G0 and G1, suggesting limited heritability of adult body size across generations. The absence of a positive correlation between the two generations can be attributed to three potential factors: 1) large variation in egg sizes produced by G0 females, 2) reduced growth efficiency in G1 individuals originating from larger G0 females compared to smaller G0 females, and 3) paternal effects, for which data were not available.

A similar phenomenon has been observed in another orthopteran insect, the migratory locust *L. migratoria* (Linnaeus, 1758). In this species, smaller females lay smaller eggs, but these eggs often produce nymphs that develop into larger adults (Tanaka and Tokuda 2024). Additionally, locusts adjust egg size depending on crowding conditions during the adult stage (Hunter-Jones 1958, Nishide and Tanaka 2019). For these insects, a positive relationship exists between female adult body size and progeny size. The production of smaller eggs by smaller females may serve as an adaptive strategy to compensate for their reduced body size in terms of fecundity without significantly influencing the adult body size of the next generation. This phenotypic plasticity likely plays a critical role in RS crickets, whose reproductive season is shortened due to submergence. The mechanisms underlying the stability of adult body size described above, warrant further theoretical investigation.

Nevertheless, considering the significant differences observed in nymphal development and adult head width under laboratory conditions, it is likely that evolutionary changes have occurred in the RS crickets over the 20–30 years since the construction of the

Oishi Dam, although further genetic analysis is needed to confirm this. However, determining whether these changes are occurring rapidly or slowly, or whether they will persist in the future, remains challenging.

Since there is no clear geographical barrier between the RS and the surrounding areas, genetic exchange with adjacent *T. emma* populations is likely. Some cricket species are known for their strong flying abilities. For instance, the two-spotted cricket *Gryllus bimaculatus* (DeGeer, 1773) begins flying within a few days after adult emergence (Tanaka et al. 1999), and adults have been recorded landing on a ship in the Atlantic Ocean, 933 km from the nearest mainland (Ragge 1972). Similarly, long-winged morphs of the tropical field cricket *Teleogryllus derelictus* (Gorochov, 1985) are capable of flight during early adulthood (Tanaka et al. 2001). Additionally, *T. emma* adults frequently fly to light traps during the summer. These observations suggest that genetic exchange be tween the RS population and adjacent populations is likely. This exchange could slow the evolutionary trends toward faster development and smaller adult sizes in the RS population.

In conclusion, the seasonal submergence of the RS of the Oishi Dam presents a unique ecological setting in which *T. emma* populations demonstrate adaptive responses through phenotypic plasticity and potential genetic differentiation. This study identified a latitudinal cline in body size contrary to Bergmann's rule, as well as year-to-year fluctuations in body size. In particular, the reservoir slope crickets of *T. emma* are subject to significant environmental constraints, including delayed hatching, shorter daylengths, and high nymphal densities, leading to reduced adult body sizes compared to adjacent grassland crickets. Laboratory experiments confirmed that rearing conditions—especially temperature and density—play pivotal roles in determining adult body size. Furthermore, photoperiodic responses suggest that shorter photoperiods accelerate nymphal development, reducing adult size, while year-to-year size variations may correlate with fluctuations in nymphal densities. Despite these environmental pressures, the absence of geographical barriers allows genetic exchange between RS *T, emma* crickets and neighboring populations, potentially tempering the pace of evolutionary change in these crickets. However, observed differences in developmental traits suggest early signs of speciation influenced by the unique conditions of the RS.

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Supplementary material 1

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Data type: xlsx
Explanation note: **table S1.** Adult morphology (mean ± SD, mm) of *T. emma* in four populations (A, B). **table S2.** Head widths of penultimate and last nymphal instars from Hirosaki, Sekikawa, and Tsukuba in 2013. **table S3. A**. Number of nymphs collected around the Oishi Dam in summer 2013. **B**. Head widths (mm) of penultimate and last instar nymphs. **table S4.** Nymphal development and adult body sizes of individuals collected from the reservoir slopes (RS), Oishi downstream park (OP), Higashimata botanical park (HP), and Sekikawa (SK) during summer 2013 and reared at 30°C under LD 14:10 h. **table S5.** Body size (mm) of adults collected from the reservoir slope (RS), Oishi downstream park (OP), Higashimata botanical park (HP), and Sekikawa (SK) during fall 2013. **table S6.** Effects of temperature and rearing density on adult body size in *T. emma*. **table S7.** Effects of rearing density on adult body size in the first laboratory generation of *T. emma* crickets. **table S8.** Photoperiodic responses at 28°C in the first (G1, A, C) and second (G2, B, D) laboratory generations of *T. emma* from reservoir slope (RS) and Sekikawa (SK). **table S9.** Adult head width (mm) of *T. emma* collected from reservoir slope (RS) and Sekikawa (SK) across different years. **table S10.** Year-to-year variations in head width and hind femur length of *T. emma* adults from Tsukuba (A), mean temperatures during May–August (B), and correlations between these variables (C). **table S11.** Relationships between the adult head width of *T. emma* females (G0) from Tsukuba and the body size of their offspring (G1). **table S12.** Air temperatures (A) and sunshine hours (B) in different years at Nakajo, Niigata (Meteorological Agency of Japan 2024).
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Link: https://doi.org/10.3897/jor.35.150472.suppl1

Supplementary material 2

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Data type: pdf
Explanation note: **fig. S1.** The developmental zero of *T. emma* post-diapause eggs and the relationship between developmental rate (100/days) and temperature. **fig. S2.** Changes in annual mean air temperature from 1964 to 2024 based on data from the Meteorological Agency of Japan (2024). **fig. S3.** Unidentified ticks found on *T. emma* adults collected at the reservoir slopes on August 1, 2013.
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